



Xue, J., Deng, Z., Huang, P., Huang, K., Benton, M. J., Cui, Y., Wang, D., Liu, J., Shen, B., Basinger, J. F., & Hao, S. (2016). Belowground rhizomes in paleosols: The hidden half of an Early Devonian vascular plant. *Proceedings of the National Academy of Sciences of the United States of America*, 113(34), 9451-9456.
<https://doi.org/10.1073/pnas.1605051113>

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Geology, Evolution

Belowground rhizomes in paleosols: the hidden half of an Early Devonian vascular plant

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27 pages; four figures; and a file of supporting information (SI)

Abstract

The colonization of terrestrial environments by rooted vascular plants had far-reaching impacts on the Earth System. However, the belowground structures of early vascular plants are rarely documented and thus the plant-soil interactions in early terrestrial ecosystems are poorly understood. Here we report the earliest rooted paleosols (fossil soils) in Asia from Early Devonian deposits of Yunnan, China. Plant traces are extensive within the soil and occur as complex network-like structures which are interpreted as representing long-lived, belowground rhizomes of the basal lycopsid *Drepanophycus*. The rhizomes produced large clones and helped the plant survive frequent sediment burial in well-drained soils within a seasonal wet-dry climate zone. Rhizome networks contributed to the accumulation and pedogenesis of floodplain sediments and increased the soil stabilizing effects of early plants. Predating the appearance of trees with deep roots in the Middle Devonian, plant rhizomes have long functioned in the belowground soil ecosystem. This study presents strong, direct evidence for plant-soil interactions at an early stage of vascular plant radiation. Soil stabilization by complex rhizome systems was apparently widespread, and contributed to landscape modification at an earlier time than had been appreciated.

Keywords: Rhizome; paleosol; clonal growth; fluvial landscape; Devonian

Significance statement

The roots and rhizomes of early vascular plants, and their interactions with soils, are poorly documented. Here we report on the complex, belowground rhizome systems of an Early Devonian plant, and their contribution to the formation of the earliest record of rooted red-bed soils in Asia. Our specimens predate the earliest trees with deep roots from the Middle Devonian by 20 million years. We propose that plant rhizomes have long functioned in terrestrial ecosystems, playing important roles in shaping Earth's environments by reducing soil erosion rates and thereby increasing the stability of land surface and resilience of plant communities.

body

The great radiation of vascular plants during the middle-late Paleozoic had profound impacts on the Earth System. The Silurian–Devonian periods witnessed a series of secular changes in Earth’s atmosphere and surface, including: decrease of concentration of atmospheric carbon dioxide; increasing prominence of meandering river facies with stabilized banks and muddy floodplains; and the increase of pedogenic sediments. These changes have been linked to the colonization of terrestrial landscapes by rooted plants (1–5). Previous studies have emphasized the effects of early trees and forests, which first appeared in the Middle Devonian (6–8), on enhanced chemical weathering rates and soil development (2, 9–11). However, the roles that vascular plants played in soil production and landscape stability prior to the evolution of trees and deep roots (the interval from ~420 Ma to 390 Ma) are poorly understood. This issue is of significance particularly in light of the ecological importance of small, herbaceous plants with a clonal growth habit in modern ecosystems (12, 13).

Early vascular plants of the Late Silurian–Early Devonian, including rhyniopsids, zosterophylloids, lycopsids and euphyllophytes, are small in aboveground stature (14, 15). While this could suggest that the belowground components of these plants were similarly small and therefore limited in their impact on sediments, fossils of their belowground structures such as roots or rhizomes are rare and incomplete (16–23). Some species have been recorded as bearing downwardly extended, shallow rooting systems (or root-like structures) (16–20), others with surficial or shallowly subterranean rhizomatous axes with rhizoids (21–23). Thus, the geochemical effect of these plants on the substrate (or soils) was presumably limited (11) and their capacity for landscape stabilization trivial. However, because of a poor fossil record, it remains quite unclear how the “hidden half” ecosystem (24), with buried structures growing in soils, functioned during the early stage of vascular plant radiation. Such a knowledge gap hinders a deep understanding of the ecology of early plants and their roles in terrestrial environments.

In this article, we report well-preserved plant traces from the Lower Devonian Xujiachong Formation of Yunnan, China, which are interpreted as representing belowground rhizomes of the primitive lycopsid *Drepanophycus*. Paleobotanical, sedimentological and geochemical studies reveal the ecology of this plant, the earliest known rooted paleosols (fossil soils) in Asia, and a mechanism for plant-soil interactions for early vascular plants.

Results

Geological setting, stratigraphy and sedimentary environments

During the Early Devonian, the South China paleocontinent was located within the paleoequatorial region and far from Laurussia (25) (Fig. 1A). The Xujiachong Formation is well exposed near Qujing City, Yunnan Province (Fig. 1 B and C; 26), and consists of predominantly terrestrial deposits ca. 600–900 m in thickness (27, 28). A late Pragian–early Emsian age has been proposed for the Xujiachong Formation in light of its plants, invertebrates and spores (27). More recently, an early Pragian to ?earliest Emsian age has been determined for the upper part of this formation based on dispersed spore assemblages of the *polygonalis-emsiensis* Spore Assemblages Biozone of Laurussia (29). In this study, we focus on the lower to middle part of this formation,

interpreted as Pragian in age (~411–408 Ma).

Outcrops and specimens have been examined at the Xujiachong, Xiaoguankou, Baojia Tunnel, and Longhua sections of the Xujiachong Formation (*SI text*; Figs. 1C, 2 and S1–S12; Table S1). The Xujiachong section has been divided into 93 sedimentary cycles (28), and this scheme is followed here. Most of these cycles show repetitive facies associations comprising: a lower conglomerate; medium to thickly bedded sandstone; thinly bedded sandstone and gray-green siltstone; and, at the top, red mudstone and gray-green siltstone/mudstone (Fig. 2A–D). Each sedimentary cycle is interpreted to represent a river channel migration or episodic crevasse splay followed by floodplain development. Intraformational conglomerates (Fig. S1), usually several centimeters thick, with abundant mud and some lithic clasts, are interpreted as basal lags of reworked floodplain deposits. Medium to thickly bedded gray sandstones, subarkosic arenitic and quartz arenitic in composition, with trough and tabular cross-bedding, ripple lamination and erosional base, are interpreted as fluvial channels and are typically found at or near the bases of some cycles (Figs. S2 and S3). Couplets of thinly bedded sandstone and gray-green siltstone occur above medium–thickly bedded sandstones or near the bases of some other cycles. Such heterolithic deposits provide strong evidence for deposition in a stabilized channel environment, either as laterally accreted point bars or crevasse splays (3, 4, 30, 31) (Figs. S2C and S4A), although in this instance outcrop limitations do not permit a conclusive discrimination among these facies. Red mudstones (paleosols) with plant traces subsequently developed as floodplain deposits (Figs. 2A–G and S7–S9). Some sedimentary cycles include red-bed paleosols 2–4 times thicker than other lithofacies in the cycle (Fig. 2 C, D and G), indicating a considerable time of landscape stability. In such cases, the sequence represents a mud-dominated, stabilized floodplain, and at Xujiachong, for example, single beds of red mudstone average 2.4 m and their sum reaches 355 m, representing ca. 42% of the thickness of the entire formation (Table S1).

Plant traces produced by *Drepanophycus*

Plant traces preserved as sediment-filled casts, molds, and/or rhizohaloes [diffuse, chemically altered zones (2, 10, 11)], occur in all lithofacies, but are most common in red and gray-green mudstone/siltstone paleosols in the examined four sections (*SI text*; Figs. 2, S4 C–H, S5 C–F, S6 A–B, S7–S11). Vertical traces are found throughout a 15.5-m-thick bed of red mudstone at Xiaoguankou (Figs. 2 F and G and S7), and similarly in Cycles 33 and 35 of the Xujiachong section (Figs. 2 C and D and S8A). The traces are more or less consistent in density and morphology through the vertical profiles, with the most common type of trace is 5.9–18 mm wide (average 10.5 mm; n = 90), and interpreted as rhizomes of the extinct, basal lycopsid *Drepanophycus*. By “rhizome” we mean vegetative extensions produced by means of axis elongation and branching either above or within the substrate. The second type is much thinner and less common, and interpreted as traces of adventitious roots of *Drepanophycus* (*SI text*; Figs. S4 G and H, and S6 A and B, arrows). Numerous traces show multiple occurrences of H- or K-shaped branchings (Figs. 2 H and I and S13), typical of the rhizomes of many zosterophylloids and early lycopsids (17, 18, 32, 33). Typically, a parent rhizome divides to produce a lateral branch at nearly 90°, and after a short distance, this lateral trace divides to

produce two daughter traces which diverge at a wide angle (K-shaped) to almost 180° (H-shaped); during this process, the trace width changes little. These are morphological expressions of the same developmental pattern, and therefore for simplicity, we refer to this pattern only as H-branching. After branching, some traces tend to extend horizontally (Figs. 2H–J, S6 A and B, and S8 B and C), while in other examples vertical traces bend to become horizontal, and in both cases appear to represent impressions of aerial plant axes (Fig. 2 I and J). Lateral, mm-scale projections can be seen on these traces (Fig. 2K), indicative of leaves. The number of trace transections on a bedding surface ranges from 800 to as high as 1300 per square meter (average 1000; Figs. S8 D and E, and S10–S11; Table S2), and the total length of rhizomes per cubic meter of sediments is estimated to be 800–1300 m. Nearest-neighbor analysis for point pattern (34) shows a statistically significant clustering (non-random distribution) of trace transections on a sampled bedding surface [$p_{\text{(random)}} \ll 0.001$].

While traces are found in both green and red beds (paleosols), gray-green mudstone/siltstone has a greater preservational potential for plant remains and may preserve coalified material (Figs. S4 F–H, and S6 C–H). In both types of beds, traces are consistent in morphology and interpreted as representing *Drepanophycus* plant (Figs. S4 F–H and S7C, S8B and S13). In many green beds, remains of *Drepanophycus* are preserved as densely arranged parallel axes (Fig. S6 C and F), indicative of effects of water currents in aligning aerial parts of the plant.

Sandstones underlying paleosols also may contain vertical and horizontal traces (Fig. S4 C–E), although less abundantly. Horizontal traces commonly occur in the bottom beds of a cycle, which truncate the underlying fines of the previous cycle, and which may preserve extensive traces (Fig. S5F). Plant traces and compression remains typical of *Drepanophycus* can be found crosscutting sandstone bedding, indicating *in situ* burial (Fig. S4 B, C and E).

The microphyllous aerial axes of *Drepanophycus qujingensis* from the Xujiachong Formation are characterized by dichotomous and pseudomonopodial branching (Fig. S6D, E and G), and appear to differ from the rhizomes on which H-branching occurs, although rhizomes may have occurred either as aerial scrambling stems or as subterranean organs. Pseudomonopodial branching means a pattern with a distinct main axis and subordinate, thinner, lateral branches (Fig. S6G), and further divisions of the lateral branches usually do not diverge with a wide angle or with opposite directions, as they do in H-branching. The width of rhizomes and their traces (average 10.5 mm) is somewhat less than that of the aerial axes of *Drepanophycus* (average 15.9 mm) (Fig. S14).

Paleosol morphology and geochemistry

Red mudstone facies (Munsell color 7.5R4/4, 10R4/2, 10R6/4), with abundant plant rhizome traces (5PB4/4, 7.5PB4/2, 7.5BG8/2) and some with scattered carbonate nodules, are classified as Protosols or Calcisols (35). Some beds of gray-green mudstone/siltstone (7.5G7/2, 10B5/2), also showing plant traces (5PB4/2, 10BG1/2) and red mottling but lacking carbonate nodules (Fig. 2I), are assignable to Protosols. Carbonate nodules are subangular to rounded in shape (Fig. S9 D and E), and in chemical components may show a sharp boundary or diffuse pattern of carbon and calcium (Fig. S12). Nodules in paleosols at Xujiachong and Xiaoguankou are 1.8–(6.7)–25.1

mm in long dimension (most commonly 3–9 mm; Fig. S15; Table S3), and show no discernable trend in size distribution versus profile depth (Fig. 2 C, D and G). While some nodules occur within, or very close to rhizohaloes, and some nodules appear to occur within distinct beds (but free from one another), most are scattered in the matrix (Fig. S9 A–D). Nodules are usually associated with local reduction of iron within the adjacent matrix. These carbonate nodules belong to developmental stage II, as measured by the criteria of Machette (nodules common, 5–40 mm in diameter) (36). The thickest exposed paleosol is 15.5 m, and as much as 17.0–19.4 m in original thickness, assuming a burial depth of 1–3 km (37), and except for some vague and discontinuous beds of carbonate nodules (Fig. S9 A and B), such paleosols show no soil profile development and seem to be aggradational (cumulate soils), lacking evidence of internal bedding or erosion.

Major and trace elemental compositions of four paleosols, three within Cycles 33, 35 and 37 at Xujiachong (9.0 m, 7.8 m, and 4.4 m thick, respectively) and one at Xiaoguankou (15.5 m), were analyzed to evaluate pedogenesis (Tables S4, S5). The homogeneity of these paleosols is verified by the molecular weathering ratio, including $[\text{Ca}+\text{Mg}]/\text{Al}$, Al/Si , $\text{Al}/[\text{Ca}+\text{Mg}+\text{K}]$, and Ba/Sr (Figs. 3 and S16), which have been commonly used to identify calcification, clayeyiness, base loss, and leaching of paleosols, respectively (2). No discernable trend is exhibited in the values of these ratios versus profile depth. The Ti/Al ratios fall within the range of mudstone-parented, weakly to moderately developed soils (38). The average weight percentage (wt%) of CaO and MgO reaches 7.48% and 4.87%, respectively, in these red-bed paleosols, and thus the calcification values are high throughout the profiles, although showing slight fluctuation that indicates some change in abundance of carbonates. Paleosol samples from the red-bed facies and two samples from adjacent green-siltstone facies are similar in molecular ratios and REE abundance (Figs. S16 and S17).

Stable isotope values of micrites of carbonate nodules ($\delta^{13}\text{C}_{\text{carb}}$ and $\delta^{18}\text{O}_{\text{carb}}$), as well as carbon isotope values of organic matter within the paleosols ($\delta^{13}\text{C}_{\text{OM}}$), show no discernable change throughout the profiles, and no significant difference between the Xiaoguankou and Xujiachong paleosols (Figs. 3, S16 and S18; Table S6). Relative to the Vienna Pee Dee Belemnite standard, the values range from -8.16 to -5.12‰ for $\delta^{13}\text{C}_{\text{carb}}$, -9.51 to -7.24‰ for $\delta^{18}\text{O}_{\text{carb}}$, and -25.28 to -23.38‰ for $\delta^{13}\text{C}_{\text{OM}}$; the difference between $\delta^{13}\text{C}_{\text{carb}}$ and $\delta^{13}\text{C}_{\text{OM}}$, $\Delta^{13}\text{C}_{\text{carb-OM}}$, averages 17.73‰ .

Discussion and Conclusions

The Xujiachong Formation presents an exceptional example of the contribution of early vascular plant vegetation to terrestrial sedimentation. Most sedimentary cycles within this formation began with a basal conglomerate or sandstone body deposited most probably by channel migration or episodic crevasse splay, followed by floodplain development.

Drepanophycus appears to have been an immediate colonizer of the newly formed alluvium, as evidenced by autochthonous or para-autochthonous preservation of abundant compression remains and plant traces in sandstone-siltstone couplets. Continuous growth of *Drepanophycus* via their rhizomes, and sequential burial in fine sediments, conferred erosion resistance to

floodplains and contributed to the establishment of red-bed paleosols. Although *Drepanophycus* is characterized by limited xylem and wide cortex tissues (16, 32, 33), the rhizomatous growth of this plant could produce dense vegetation cover (Fig. S19), which alone would have protected the substrate against surface erosion while increasing trapping of fine particles (4, 39), as has been demonstrated in numerous studies of the erosion-reducing effects of modern plants (5, 39). Perhaps more importantly, belowground rhizomes of *Drepanophycus* formed complex networks as a result of belowground growth as well as sequential burial of aerial stems and rhizomes, which had the potential to bind sediments in a reinforced matrix (Figs. S10 and S11), thereby increasing soil aggregate stability. Analogous cases are common in modern environments, where for example the angiosperms *Psammochloa villosa* and *Sporobolus virginicus* form dense rhizomatous networks that are subject to frequent burial, and efficiently stabilize mobile sand dunes (13, 40). Other factors may have contributed to stabilization, including decomposition of *Drepanophycus* rhizomes, a source of organic matter that would increase the soil structure, and, in some cases, contribute to formation of rhizocretions (Fig. S10 B and D) to provide additional resistance against erosion.

Quantifying the effects of roots (or rhizomes) on soil erosion rate is difficult, due to the diversity of root architectures and soil structures. However, root volume and root length per unit of sediments (root length density) are two variables that can be compared across communities and can be obtained from the fossil record (but only in rare cases, as in this study). Experiments have shown that bank sediments with 16–18% roots by volume can have 20,000 times more resistant to erosion than those without vegetation (41). For reference, in this study rhizomes of *Drepanophycus* are estimated to have occupied 6.9–11.3% by volume of sediment (Table S7). Root length density (RLD) has been found to correlate well with the soil detachment ratio (SDR) (*SI text*; 39). The rhizome length density within the Xujiachong paleosols is estimated to be 0.8–1.3 km/m³, a value at the lower range of modern plant roots (39), and by using the non-linear regression function between RLD and SDR resulting from concentrated flow (39), weak to modest effects of rhizomes in reducing soil erosion can be expected (*SI text*; Table S8).

The mud-dominated beds of the Xujiachong Formation are interpreted as the result of long-term development of floodplain deposits, where an individual aggradational paleosol sequence may reach up to 20 m thick and contain abundant plant traces and carbonate nodules of stage II development of Machette (36). Episodic overbank flooding, with high aggradation rates of 10–40 mm a⁻¹, has been proposed as a dominant mechanism in forming these types of alluvial deposits on floodplains (42). Given these conditions, development of an active pedogenesis zone 2 m thick would require 50–200 years, and during aggradation plants appear to have recovered from the buried plant body, given the vertical continuity of many of the *Drepanophycus* traces. The lifespan of a *Drepanophycus* clone may have been on the order of decades or even centuries, if this fossil plant was similar in its clonal growth to the related extant lycopsid *Lycopodium*, or the fern *Pteridium* (Table S9). However, the stage II carbonate nodules within these paleosols imply a much greater residence time of 10,000–200,000 years (43). Thus, multiple generations of *Drepanophycus* clones would have grown within the beds, with periodic deposition by episodic flooding events and very long intervals of active pedogenesis with little deposition.

Paleosols of the Xujiachong Formation and their pedogenic carbonates document the earliest record of plant-influenced pedogenesis in Asia (44), and our findings are consistent with this earlier report. These paleosols were aggradational, with poor horizonation [Protosols, comparable to modern Entisols or Inceptisols (35)], some bearing a high proportion of carbonate nodules [Calcisol (35)]. Geochemical proxies for calcification ($[\text{Ca}+\text{Mg}]/\text{Al}$), clayeyness (Al/Si), base loss ($\text{Al}/[\text{Ca}+\text{Mg}+\text{K}]$) and leaching (Ba/Sr) confirm their homogeneity, deposited under a seasonal, wet-dry climate as indicated by the presence of pedogenic carbonate (44, 45). The abundance of carbonate, in terms of calcification $[\text{Ca}+\text{Mg}]/\text{Al}$ index, is ten times higher than most of the Middle Devonian forest soils of New York, USA (10). Such high concentrations of Ca^{2+} and Mg^{2+} indicate carbonate accumulation on a geomorphologically stable landscape over a long time, i.e., at least thousands of years (36).

The $\delta^{13}\text{C}_{\text{carb}}$ values of the carbonate nodules from the Xujiachong paleosols (-8.16 to -5.12‰) are similar to those of the North American Bloomsburg Formation (Silurian) and Catskill Formation (Upper Devonian), implying a strong contribution of ^{13}C -rich atmospheric CO_2 to the carbonate $\delta^{13}\text{C}$ (46) and, thus, a well-drained soil (47). The organic matter within the Xujiachong paleosols has a $\delta^{13}\text{C}_{\text{OM}}$ value of -25.28 to -23.38‰ , consistent with the $\delta^{13}\text{C}$ of coeval vascular plants including *Drepanophycus* (48). The consistently high $\Delta^{13}\text{C}_{\text{carb-OM}}$ values through the profile depth, averaging 17.73‰ and larger than values for the supposed equilibrium difference between carbonate and soil organic matter (12.2 – 15.8‰), indicate low soil productivity during the formation of the pedogenic carbonates (49).

The new knowledge of plant traces and paleosols of the Xujiachong Formation contributes to the interpretation of some previous records. Extensive traces preserved as casts in alluvial deposits of the Lochkovian–Pragian of South Britain, some also seemingly with H-branching, were interpreted as produced by the fungus *Prototaxites* (50). Some of the large plant traces from the Battery Point Formation (Emsian) of Gaspé, Canada, were described as roots and rhizomatous extensions extending downward into the substrate nearly 1 m, and interpreted as evidence of deep rooting (although the parent plant is unknown, *Drepanophycus* has been suggested as one of the candidates) (51). Evidence from the Xujiachong Formation suggests that the traces do not represent downwardly extended roots, but rather belowground rhizomes of *Drepanophycus* and progressive burial of a long-lived plant body. We speculate that a similar explanation may account for the remains in South Britain and Canada, where compression remains of *Drepanophycus* are also encountered (50, 51). Paleosols are abundant in the Upper Silurian and Lower Devonian of Laurussia, for example in Lower Old Red Sandstone facies of Britain (31, 52). While most British profiles clearly show soil horizon development (e.g., Vertisols), some resemble the Xujiachong paleosols in the presence of vertically aligned drab haloes and stage II carbonate nodules (31).

The extension of rhizomes to produce large clones seems to have been well established in Silurian–Devonian floras (Fig. 4A) (53). The rhizomatous clonal habit of *Drepanophycus* has been demonstrated by previous studies, and the belowground rhizomes of this plant spread out and colonized space via repeated H-branching as the plant grew (32, 33). We show that such rhizomes developed in vertical profiles, within unexpected thicknesses in a setting of prolonged

accumulation of sediment. The existence of clonal growth similar to that of *Drepanophycus* is known to have occurred among Pragian zosterophylloids, and has been demonstrated clearly for *Bathurstia* (17, 18). Rhizomatous habit also occurred in the Early Devonian rhyniopsids (21, 22), early euphyllophytes, and other groups (14). Most Rhynie Chert plants of Early Devonian age have rhizoid-based rhizomatous axes, which are either surficial or shallowly subterranean at a mm-scale depth (22, 23). Large woody rhizomes of aneurophytalean progymnosperms have been found in the Middle Devonian of New York, USA, alongside cladoxylopid and lycopsid trees (7). Rhizomes characterized many Late Devonian plants, including fern-like clades (15). For plants with small and ephemeral aboveground structures, rhizomatous clonal growth contributes to robustness, as evidenced here in *Drepanophycus*, and survival in disturbed environments, in particular where they are subject to frequent sediment burial.

The Lower Devonian Xujiachong paleosols and plant traces provide strong, direct evidence for plant-soil interactions during the Early Devonian. Predating the earliest trees, the rhizomes of early vascular plants such as *Drepanophycus* would have contributed to stabilization of fluvial sediments and floodplains, and in some cases formed a deep soil ecosystem that would have served as an important carbon sink and a place for the diversification of terrestrial invertebrates. The proportion of meandering river facies, with stabilized banks, muddy floodplains, rooted sediments, and pedogenic carbonate nodules, increased steadily in the geological record from the Late Silurian (Fig. 4B), reflecting a secular change in fluvial geomorphology (3–5). This change in terrestrial landscapes paralleled the evolution of vascular plants and the expansion of vegetation cover (Fig. 4C). We propose that, underlying these processes, belowground rhizomes of early plants such as *Drepanophycus* were one of the biological agents working on landscape evolution by moderating soil erosion. Plant rhizomes persisted as a strategy into later geologic periods, as evidenced by the Middle Devonian aneurophytalean forests with woody rhizomes [Gilboa, USA (7)], and they continue to play critical roles in modern ecosystems (12, 13).

Acknowledgements. This work was supported by the National Natural Science Foundation of China (No. 41272018), Yunnan Key Laboratory for Palaeobiology, Yunnan University (No. 2015DG007-KF04), and Key Laboratory of Economic Stratigraphy and Palaeogeography, Chinese Academy of Sciences (Nanjing Institute of Geology and Palaeontology). We are grateful to Prof. Martin Gibling and Dr. Neil Davies for their correspondence about fluvial deposits and the anonymous reviewers for their constructive comments.

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Figure legends

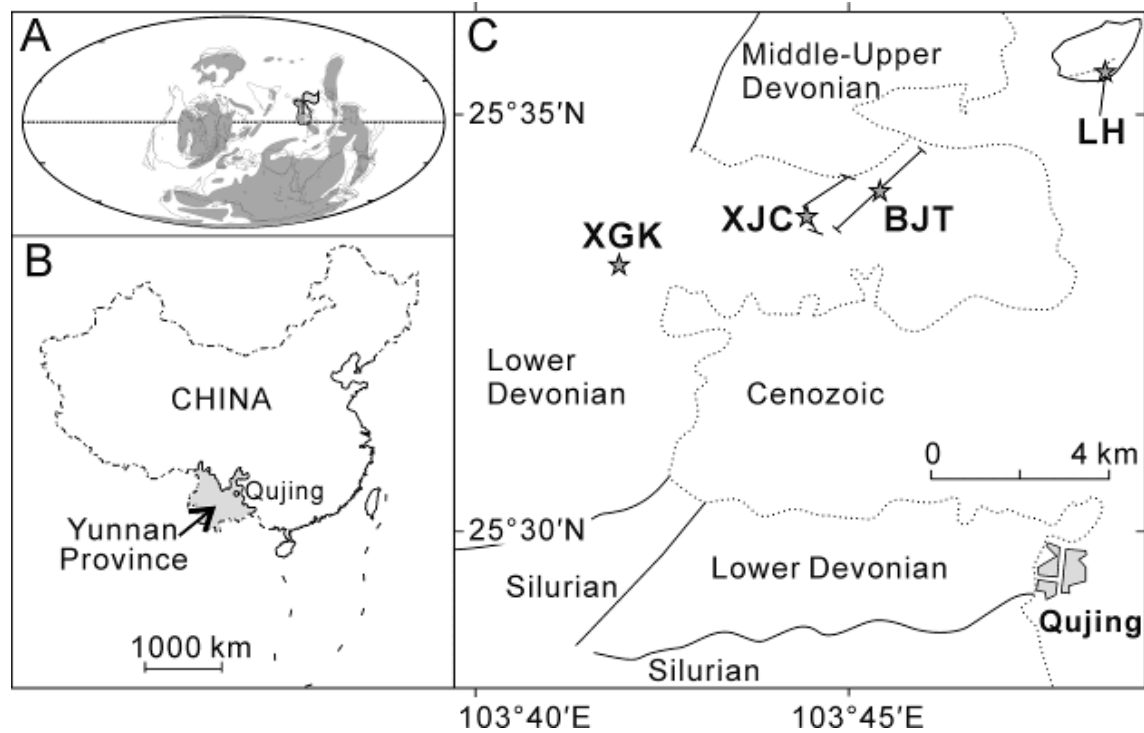


Fig. 1. Location and geologic map. (A) Early Devonian paleomap showing the location of South China (25). (B and C) Location and geology of the study area, near Qujing, Yunnan Province, China. The studied sections of the Lower Devonian Xujiachong Formation at Xujiachong (XJC), Xiaoguankou (XGK), Baojia Tunnel (BJT), and Longhua (LH) are indicated by stars.

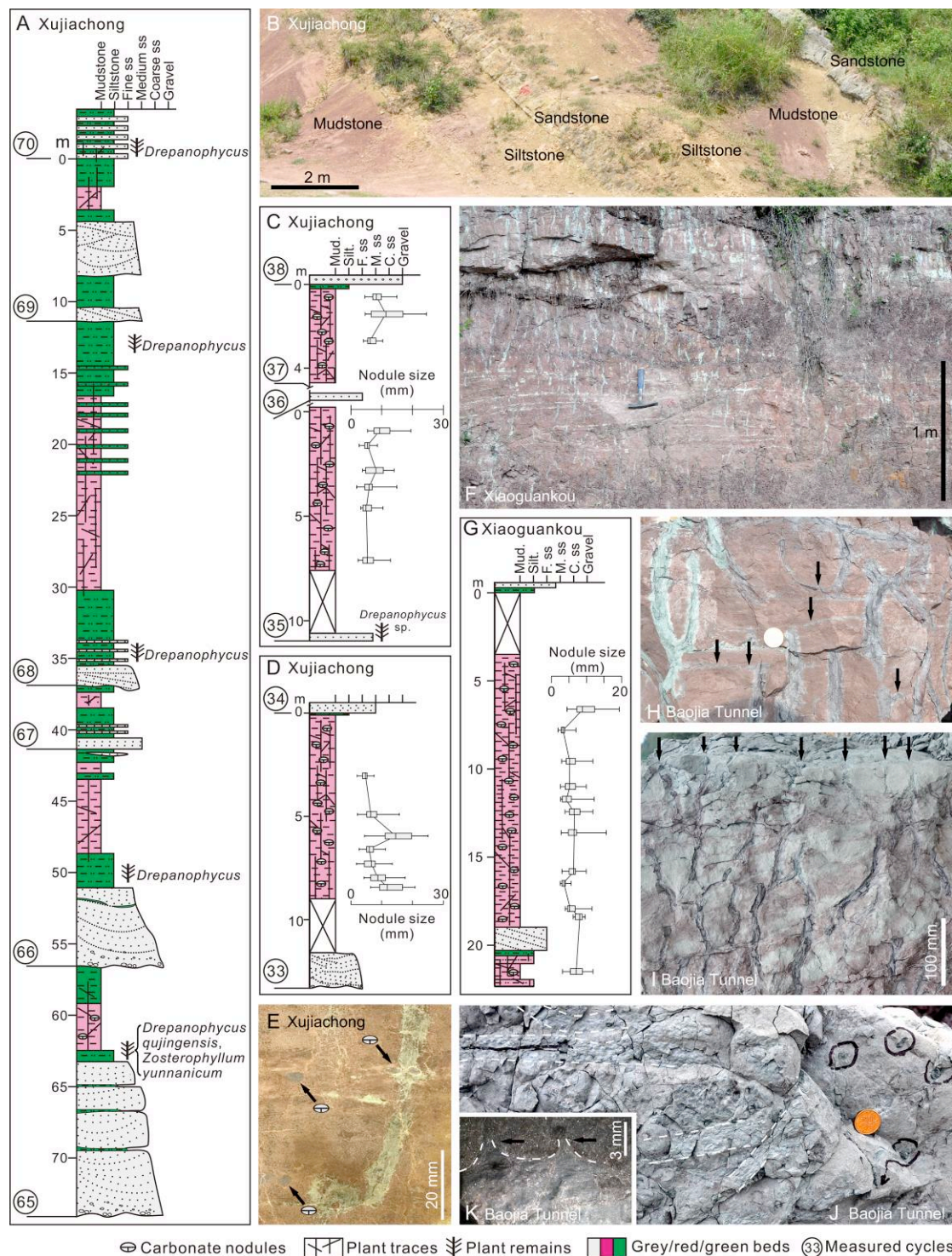


Fig. 2. Stratigraphy of the Xujiachong Formation. (A, C, D, G) Lithological columns with representative sedimentary cycles of the Xujiachong section. Cycle numbers, lithofacies, and contained fossil plants are based on ref. 28 and our re-examination. (B) Typical sedimentary sequence at Xujiachong. (E) Polished vertical section of red mudstone (at Xujiachong), with drab-haloed plant traces and scattered carbonate nodules (arrows). (F) Red mudstone with green

vertical plant traces at Xiaoguankou. (G) Stratigraphy of the Xiaoguankou section. (H–K) Specimens from the Baojia Tunnel section. (H) Gray-green vertical traces in red mudstone, with K- or H-type branching and horizontal extension (arrows). (I) Vertical traces in green mudstone with red mottling. Traces bend to horizontal on upper surface, the edge of which is indicated by arrows. (J) Upper surface of the rock in (I). Traces with horizontal extensions (weak contrast with the matrix) and transections (black circles). (K) Vestige of axes with lateral projections (arrows). (Scale: coin in H and J, 20 mm).

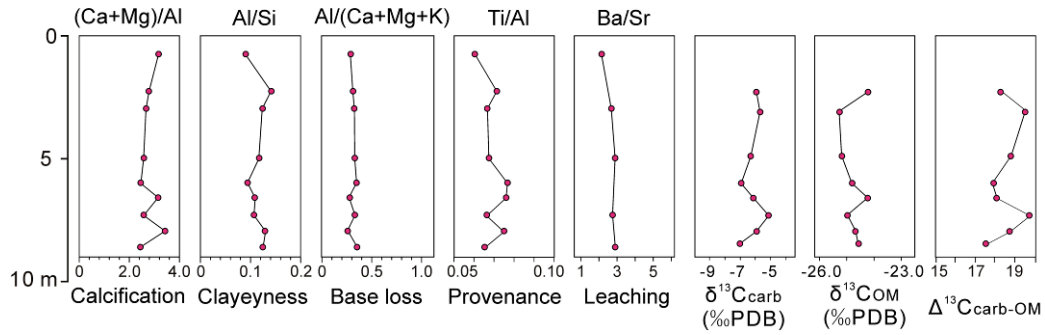


Fig. 3. Geochemical characteristics of a paleosol of the Xujiachong Formation (Cycle 33 at Xujiachong, see Fig. 2D for lithology). $\delta^{13}\text{C}_{\text{carb}}$, stable carbon isotope values of carbonate nodules; $\delta^{13}\text{C}_{\text{OM}}$, stable carbon isotope values of organic matter within the paleosol; $\Delta^{13}\text{C}_{\text{carb-OM}}$, the difference between $\delta^{13}\text{C}_{\text{carb}}$ and $\delta^{13}\text{C}_{\text{OM}}$.

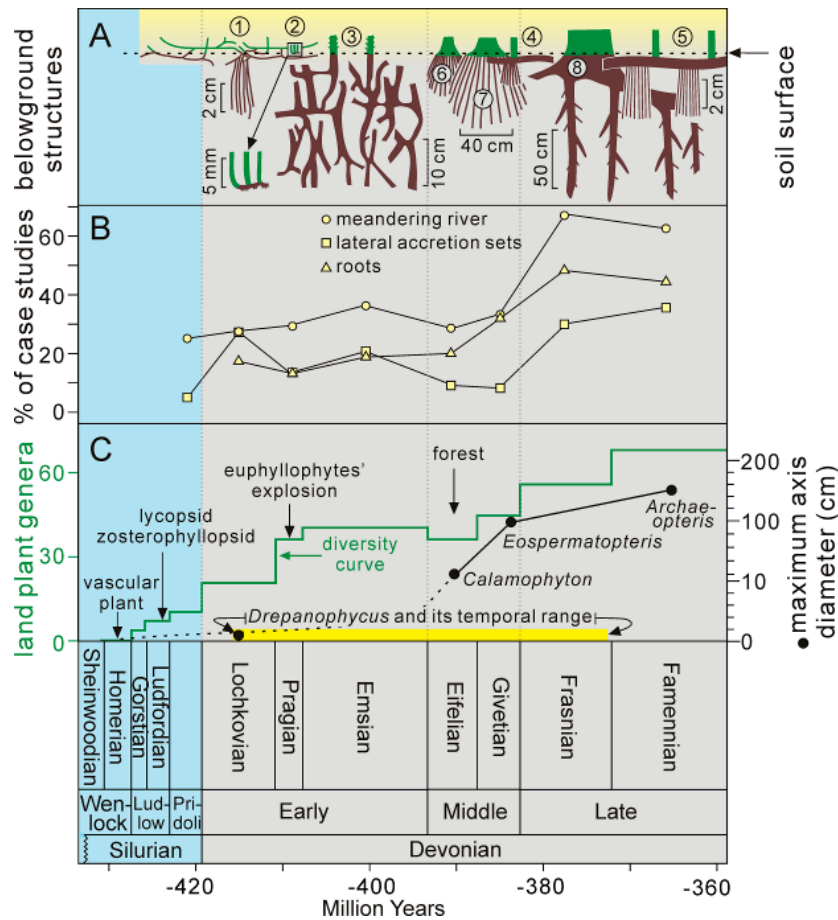


Fig. 4. Vascular plant and geomorphological evolution during the Silurian–Devonian. (A) Belowground structures of representative plants; most are characterized by rhizomes [1: *Zosterophyllum* (19); 2: *Rhynia* (22); 3: *Drepanophycus* (Pragian in this study, but widespread in Early Devonian); 4: aneurophytalean (7); 5: fern-like plants (15)], while some are trees with roots [6, 7: pseudosporochnalean (7, 8); 8: archaeopteridalean (9)]. (B) Percentage of fluvial successions with meandering river facies, lateral accretion sets, and plant rooting structures (3). (C) Plant diversity (54), key evolutionary events, maximum size of plant axes (6), and temporal range of *Drepanophycus*.